

## FORECAST OF A SYSTEM OF THE DICOTYLEDONS

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A standing problem of taxonomic biology — its importance and difficulty made known by the incompletely successful efforts of fully two centuries — is that of the natural and convenient organization of the families of dicotyledons in groups of the category of orders. De Candolle (1813; to him, what we call a family was an order, and what we call an order was a subclass, legion or cohort) remarked of this problem, "C'est là le problème le plus important à résoudre qui se présente aujourd'hui dans l'étude des rapports naturels." And Schnarf (1933) had still to say, "Dagegen ist die Gruppierung der Familien zu Ordnungen oder Reihen schon mit einer gewissen Unsicherheit behaftet, die darin zum Ausdruck kommt, dass die Abgrenzung der Ordnungen von verschiedenen Forschern vielfach in verschiedener Weise vorgenommen wird."

In his work just cited, De Candolle observed that there had been almost as many systems as systematists; which is not far from saying that every systematist has a right to his own system. Among the very many systems which systematists have produced, few have had much influence. During the nineteenth century, the system of De Candolle (of which that of Bentham and Hooker is a variant) overshadowed all others; subsequently, the system of Engler and Prantl has had the same effect. All this is as it should be. We need at every time to have an accepted system, by which we may know where to look for what concerns us in herbaria and manuals. The systems which have been offered as challenges to the accepted systems have brought about minor improvements in the latter. They have had the more important effect of keeping us aware that the accepted system is never the final truth. As the system of Engler and Prantl displaced that of De Candolle, so surely it will be displaced by one which is recognizably a more satisfactory representation of the system which exists in nature.

Considering these things, I took a summons to appear in a symposium as occasion to try to predict the system of the future; this to the extent of formulating the skeleton of a system which is set forth below.

This system gives much weight to microscopic characters, though I can scarcely claim mastery of the great mass of available data. Metcalf and Chalk (1950) give a bibliography of about twenty-five hundred titles, nearly all of them subsequent to the translation of Solereder by Boodle and Fritsch (1908). Schnarf (1931) listed about seventeen hundred contributions to embryology. Wodehouse (1935) listed some three hundred

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<sup>1</sup> It was a high honor, accepted with diffidence, to be asked to speak on "Anatomy and taxonomy" in a symposium commemorating the fiftieth anniversary of the Botanical Society of America, on August 28, 1956, at the meeting of the American Institute of Biological Sciences at the University of Connecticut. The present paper is a revision of the one given on that occasion.

papers on pollen grains, and Erdtmann (1952) about eleven hundred in the same field. Where study of vascular anatomy, at Harvard and elsewhere, has yielded definite conclusions, it has been possible to formulate orders with considerable confidence; for the rest, the orders are those of Engler and Prantl with certain amendments suggested by embryological or palynological data.

Large orders are preferred to small: in maintaining an order of two or three families, one is not far from leaving the families unplaced. However, it has not been found possible to be consistent in this matter. It is not considered necessary that the orders be definable by description.

Names are applied to the orders according to the principles of priority and typification. The experience of very many taxonomists has shown it necessary to apply these principles in dealing with genera and species. Experience with the formulation and naming of higher groups has been comparatively scant. Perhaps for this reason, taxonomists in convention have taken the position that it is possible to make defensible choices among the fairly numerous names which have been applied to higher groups without recourse to the principles cited. Whether or not this position is sound, no novelties are here added to the synonymy of ordinal names.

#### Subclass DICOTYLEDONES Lindley

Synops. British Fl. 4 (1829).

Order 1. MULTISILIQUAE L. Gen. Pl. ed. 6 (1764). Orders *Piperitae* and *Coadunatae* L. op. cit. Orders *Piperinae* (Brongniart, as class) and *Polycarpicae* (Endlicher, as class) Braun in Ascherson Fl. Brandenburg 1: 36, 47 (1864). Orders *Piperales* and *Ranales* Engler Syllab. 93, 106 (1892).

Among names of the three natural orders in which Linnæus placed these plants, that of which the apparent typical genus is *Ranunculus* is preferred to those of which the apparent typical genera are respectively *Piper* and *Magnolia*.

This order includes the generality of dicots with apocarpous flowers, as well as some of their immediate derivatives. They have been studied extensively by Bailey and his associates (Bailey and Nast, 1943, 1944, 1945; Bailey, Nast, and Smith, 1943; Bailey and Smith, 1942; Bailey and Swamy, 1949; Smith, 1943, 1945, 1946, 1947; Swamy, 1949; Swamy and Bailey, 1949). These scientists are authority for the assemblage here of a large number of families, including the Piperaceæ and their immediate allies. To current botanical opinion, this is definitely the primitive order of flowering plants. Some families are homoxylous, *i. e.*, having wood without vessels, in contrast to the heteroxylous condition which is characteristic of flowering plants. In some families the pollen grains are monocolpate, *i. e.*, marked by a single groove; this character they share with the generality both of the lower seed plants and of the monocots, while in typical dicots the pollen grains are tricolpate or of more elaborate types derived from this. The two primitive characters mentioned, and the peculiar

anatomical character of oil cells in the tissues, are distributed among the families of Multisiliquæ each one in seeming independence of the others. This means that, quite as one would expect of a primitive group, the families are isolated or fall into isolated blocks. It is necessary as a matter of convenience to maintain the order as a whole; it is not possible to divide it into a small number of natural orders. The families are as follows:

- a. Homoxylous, pollen monocolpate: Winteraceæ.
- b. Heteroxylous, pollen monocolpate: Degeneriaceæ, Himantandraceæ, Magnoliaceæ, Anonaceæ, Eupomatiaceæ, Myristicaceæ, Canellaceæ, Monimiaceæ, Gomortegaceæ, Lauraceæ, Hernandiaceæ, Lactoridaceæ, Calycanthaceæ, Chloranthaceæ, Piperaceæ, Saururaceæ.
- c. Wood degenerate, pollen monocolpate: Nymphæaceæ (pollen tricolpate in subfamily Nelumbonoideæ).
- d. Homoxylous, pollen tricolpate: Trochodendraceæ, Tetracentraceæ.
- e. Heteroxylous, pollen tricolpate: Eupteleaceæ, Cercidiphyllaceæ, Illiciaceæ, Schisandraceæ, Berberidaceæ, Menispermaceæ, Lardizabalaceæ, Ranunculaceæ.

Order 2. JULIFLORÆ (Endlicher as class) Braun in Ascherson Fl. Brandenburg 1: 62 (1864). Order *Amentaceæ* of Linnæus and Jussieu: one would not maintain a name in *-aceæ* as that of an order. Tippe (1938), on the basis of studies of the anatomy of the wood, assembled the families Hamamelidaceæ, Platanaceæ, Myrothamnaceæ, Stachyuraceæ, Betulaceæ, Fagaceæ, and Casuarinaceæ, as a natural group derived immediately from Multisiliquæ.

It is an annoyance to have no definite opinion as to the natural place in the system of the familiar families Salicaceæ and Juglandaceæ. Gundersen (1950) grouped Juglandaceæ with Myricaceæ and Rhoipteleaceæ, which may well be sound; but there is not much to tell where the group belongs.

Order 3. SCABRIDÆ L. Order *Urticæ* Jussieu, the mere plural of a generic name. Order *Urticinæ* (Bartling as class) Braun. Order *Urticales* Engler Syllab. 95 (1892). Ulmaceæ, Eucommiaceæ, Moraceæ, Urticaceæ. Study of the woods by Tippe (op. cit.) was held to confirm this generally-accepted group as natural, and to show that its origin was from the lower Julifloræ.

Order 4. GUTTIFERÆ Jussieu Gen. Pl. 225 (1789). Suborder *Theineæ*, Theaceæ, Marcgraviaceæ, Caryocaraceæ, Medusagynaceæ, Clusiaceæ, Hypericaceæ, Quiinaceæ, Eucryphiaceæ, Ochnaceæ, Dipterocarpaceæ. Vestal (1937) found the anatomy of the woods to confirm as natural this generally accepted assemblage of families. They show nice transitions from primitive vessels with barred perforations to advanced vessels with porous perforations. Similarly in the flowers, there are transitions from spiral parts of indefinite numbers to whorled parts of definite numbers, while the endosperm varies from nuclear to cellular (Schnarf on *Saurauia*, 1924; Swamy on *Marcgravia*, 1948). The basic family Dilleniaceæ is

needed to bind together this assemblage; it might otherwise as well be included in Multisiliquæ.

Order 5. BICORNES L. Orders *Rhododendra* and *Ericæ* Jussieu Gen. Pl. 158, 159 (1789). Order *Ericales* Engler Syllab. 151 (1892). The vessel perforations vary in the Bicornes from barred to porous. The flowers are characteristically sympetalous (there are both primitive and derived examples with separate petals); the stamens are free of the corolla, with no ribbed endothecium (except in the primitive family Clethraceæ), the anthers opening through pores, the pollen grains united in tetrads. The endosperm is cellular: the first two divisions of the endosperm mother cell are transverse, producing a row of four cells, among which the terminal members give rise to haustoria. Nearly all authorities agree that this group is immediately related to *Saurauia*, which belongs in or next to Actinidiaceæ. The families are Clethraceæ, Ericaceæ, Empetraceæ, and Epacridaceæ. In many Epacridaceæ, the stamens are epipetalous and the anthers open through slits, and the pollen grains are solitary; but these plants are linked to Ericaceæ by clear lines of transition. The families Lennoaceæ and Diapensiaceæ, which have been placed in this order, do not belong to it, and are for the present left unplaced.

Order 6. GUIACANÆ Jussieu Gen. Pl. 155 (1789). Order *Diospyrinæ* (Brongniart as class) Braun in Ascherson Fl. Brandenburg 1: 37 (1864). Order *Ebenales* Engler Syllab. 155 (1892). Styraceæ, Sapotaceæ, Symlocaceæ, Ebenaceæ, and other families. De Candolle condemned *tatonnement* (fumbling!) as a method of recognizing the natural system; yet it was the accident that I have *Styrax* in near-by foothills and a plant of *Camellia* in my back yard that enabled me to see that Styraceæ is immediately related to Theaceæ.

Order 7. PASSIFLORINÆ (Brongniart as class) Braun in Acherson Fl. Brandenburg 1: 50 (1864). Order *Rotaceæ* L., in part. Order *Cisti* Jussieu, the mere plural of a generic name. Order *Parietales* (Endlicher) Braun op. cit. 49. *Cistifloræ* Eichler. Vestal (1937) assembled the families Flacourtiaceæ, Bixaceæ, Cochlospermaceæ, and Cistaceæ as a natural group descended directly from Multisiliquæ. Whether the herbaceous families Passifloraceæ, Caricaceæ, Cucurbitaceæ, and Begoniaceæ, usually placed with these, belong with them or belong together, and whether Violaceæ and Resedaceæ belong with them, is apparently as yet uncertain.

Order 8. SENTICOSÆ L. op. cit., the evident standard genus being *Rosa*. Orders *Papilionaceæ*, *Lomentaceæ*, and *Pomaceæ* L. Order *Rosifloræ* (Endlicher) Braun. Order *Rosales* Engler Syllab. 115 (1892). Tippon (1938) showed that Saxifragaceæ *sens. lat.*, Brunelliaceæ, Cunoniaceæ, and Rosaceæ belong together. Presumably Crassulaceæ, Pittosporaceæ, and Leguminosæ belong with them. They are derived directly from woody Multisiliquæ.

Order 9. RHOEADAEAE L., including orders *Corydales*, *Putamineae*, and *Siliquosae* L. Order *Rhoeadinae* (Bartling as class) Braun. Order *Rhoeadales* Engler Syllab. 111 (1892). Papaveraceae, Tovariaceae, Fumariaceae, Capparidaceae, Cruciferae; Moringaceae and Violaceae have been placed here. They are believed to be derived directly from Multisiliquae.

To this point in this presentation, it is believed that the truth as to the main outline of the phylogeny of the dicots has been perceived. The order Multisiliquae is primitive; Juliflorae, Guttiferae, Passiflorinae, Senticosae, and Rhoeadae are immediate derivatives; Scabridae, Bicornes, and Guaiacanae are secondary derivatives. A considerable number of further orders are recognizable, but their connections are less clear. Gundersen (1950) took note that most compound pistils with axile placentation pass during development through a stage in which the placentation is parietal. Considering this fact in connection with the principle that ontogeny recapitulates phylogeny, he thought it probable that the group here called Passiflorinae is an important secondary center of variation, ancestral to most of the remaining dicots. It is arguable, on the contrary, that parietal placentation is not usually a primitive character, but a result of pædogensis, that is, of courses of evolution by which the immature condition of a relatively primitive organism becomes the mature condition of its derivatives. Hallier (1905) would have derived many of the more advanced dicots from Sterculiaceae. Purely as a speculation, it is here suggested that more orders than Bicornes and Guaiacanae may be derived from Guttiferae.

Order 10. PRECIAE L., including orders *Rotaceae*, *Caryophyllei*, and *Holoraceae* and *Succulentae* L. in part. Orders *Curvembryae*, *Centrospermae*, *Polygonales*, *Opuntiales*, *Primulales*, and *Plumbaginiales* of Engler and others. A matter of fifteen families, decidedly varied in gross characters. The bulk of the families are characterized by curved or coiled embryos. Schnarf (1931, 1933) found Opuntiaceae definitely linked to these, perhaps in the neighborhood of Aizoaceae, by embryological characters. The embryos are straight or nearly so in Polygonaceae (in which the anatomy of the stem is anomalous, as it is also in Amaranthaceae and Chenopodiaceae), Primulaceae (notably similar to Caryophyllaceae in gross features) and Plumbaginaceae (distinguished by embryological peculiarities).

In the middle of the Englerian system of the dicots, there is a long series of families, from Pandaceae to Cynomoriaceae, of which the majority are mere names to European and North American field botanists. Engler assembled many of these as two orders distinguished by the position of the ovules. In Geraniales, the ovule is epitropous, "turned up," either erect with the micropyle turned in or pendant with the micropyle turned out. In Sapindales, the ovule is apotropous, "turned down," either erect with the micropyle turned out or pendant with the micropyle turned in. The extensive study of woods principally of these families by Heimsch (1942) appears to have revealed a more natural grouping than the Englerian: the next three orders represent it.

Order 11. POLYGALINÆ (Brongniart as class) Braun in Ascherson Fl. Brandenburg 1: 36 (1864). Order *Polygalales* (Bessey as suborder, 1897) Hallier (1905). Wood with rays heterogeneous I or II A; parenchyma in apotracheal bands or scantily paratracheal; fiber-tracheids with conspicuously bordered pit-pairs. Humiriaceæ, Linaceæ, Erythroxylaceæ, Polygalaceæ, Krameriaceæ, Diclidantheraceæ, Trigoniacæ, Tremandræceæ, Zygophyllaceæ, Malpighiaceæ, Vochysiaceæ.

Order 12. TRIHILATAE L. Order *Terebinthinae* (Bartling) Braun. Order *Terebinthales* Wettstein. *Pinnatæ* Hutchinson. Rays heterogeneous II B or homogeneous; parenchyma banded or paratracheal; wood fibers with simple pits. Rutaceæ, Cneoraceæ, Simarubaceæ, Meliaceæ, Sapindaceæ, Hippocastanaceæ, Aceraceæ, Bretschneideraceæ, Connaraceæ, Burseraceæ, Terebinthaceæ. Julianiaceæ is to be reduced to Terebinthaceæ.

The action of botanical congresses in conserving numerous names of families was scarcely duly considered, since practically all of these names are valid by the letter of the code. As an exception, the name Terebint(h)aceæ (Jussieu as order) appears to have been applied definitely to a family before Anacardiaceæ was.

Order 13. GRUINALES L. Order *Geraniales* Engler. The wood (of woody examples) exhibits advanced characters, absence of scalariform perforations and presence of libriform fibers. Geraniaceæ, Oxalidaceæ, Tropæolaceæ, Balsaminaceæ. Limnanthaceæ, a small family of herbs of western North America, are in gross structure closely similar to Geraniaceæ. They are embryologically peculiar (having a 4- or 2-sporic embryo sac of unique type; Mason, 1951; Mathur, 1956), but may as well be placed here.

Order 14. TRICOCCEAE L. Euphorbiaceæ, an enormous family, chiefly tropical, grossly varied in every character as though not a natural group.

Order 15. COLUMNIFERAE L. Order *Malvales* Engler. Tiliaceæ, Malvaceæ, Bombacaceæ, Sterculiaceæ, and other families; a thoroughly natural group.

Order 16. CALYCANthemAE L. Orders *Calycifloræ* and *Hesperideæ* L., in part. Order *Myrifloræ* (Endlicher) Braun. Loasaceæ, Thymelæaceæ, Elæagnaceæ, Lythraceæ, Onagraceæ, Melastomaceæ, Myrtaceæ, and many others; needing further study.

Order 17. UMBELLATAE L. Order *Hederaceæ* L., in part. Order *Umbellifloræ* (Bartling as class) Braun. Cornaceæ, Araliaceæ, Umbelliferae. The suggestion that Garryaceæ also belongs here has been confirmed by a recent thorough study by Moseley and Beeks (1956).

Order 18. SANTALINAE Grisebach. Like Calycanthemae and Umbellatæ, these have choripetalous flowers with inferior ovaries; the characters may be obscured by reduction. Olacaceæ, Santalaceæ, Loranthaceæ, Balanophoraceæ, etc.

Among sympetalous dicots, the Bicornes, Guaiacanæ, and Primulales

have already been given places. As to the remainder, the evidence, particularly from the embryology, inclines one to treat them as a natural group of four orders, as follows.

Order 19. LURIDÆ L., including orders *Campanacæ* L. (Convolvulacæ and Polemoniaceæ), *Personatæ* L. (Scrophulariaceæ, etc.), *Asperifoliæ* L. (Hydrophyllacæ and Boraginacæ) and *Verticillatæ* L. (Labiata). Order *Tubifloræ* (Bartling as class) Braun. About twenty-three families. In Bicornes and Guicacanæ, the cellular endosperm is inherited from certain Guttiferæ. In the present order it has evolved separately, the lower families, Convolvulacæ and Polemoniaceæ, having nuclear endosperms. Whereas in Bicornes the endosperm mother cell undergoes two transverse divisions and produces a linear four-celled endosperm, in the present order it undergoes usually a transverse division followed by a longitudinal division, producing a T-shaped stage. The apetalous family Callitrichacæ has the embryogeny of this group.

Order 20. CONTORTÆ L., including *Sepiariæ* L. Seven families, a very natural group, apparently a minor offshoot of the preceding.

Order 21. STELLATÆ L. Caprifoliaceæ and Rubiaceæ. The Adoxaceæ have the pollen of this group (Erdtmann, 1954).

Order 22. AGGREGATÆ L. Eight families, including Campanulacæ, Lobeliaceæ, Valerianaceæ, Dipsacaceæ, and Compositæ. In the Englerian system, part of these are in Rubiales, but the embryological characters (and, indeed, the characters in general) place them as here.

A large number of families remain unplaced. Places could be given to many of them by recognizing such orders as Juglandales, Aristolochiales, Sarraceniales, and Celastrales; but these are either small and themselves not certainly placed, or else not evidently natural. Surely, by sufficient study of anatomy, embryology, and palynology, we will eventually learn their true positions.

At the same meetings and on the same day on which this paper was given oral presentation, Dr. Arthur Cronquist presented a system of the dicots which is expected soon to reach publication. Cronquist places all of the families in orders, which, for the sake of definition by description, are made considerably smaller and more numerous than the ones here maintained. The orders are arranged in a phylogenetic pattern with which the one here presented is in essential agreement so far as it goes. The differences between his system and mine are as though we were artists representing the same tree under the conventions of different schools, and as though he had seen many more details than I (I have every reason to believe that he has perceived most of them correctly). The points of agreement allow us to believe that we are actually approaching the system of the future.

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## A BOTANICAL DISASTER

ERWIN F. LANGE

A chance meeting of two botanical explorers along the shores of the Columbia near The Dalles, Oregon, on November 13, 1843, left a story of disaster which completely altered the life of a German botanist, Frederick George Jacob Lueders. For on that day Lueders stood by helplessly as he watched the turbulent Columbia swallow up his entire botanical collection and collecting equipment. In a matter of seconds the results of three years' labor in the wild and mountainous parts of the United States were washed away. All that Lueders was able to rescue from the water was a treasured copy of his Torrey and Gray Flora.<sup>1</sup> This event would probably have gone unrecorded in the pages of Northwest science history had it not been for the famed United States explorer, Captain John C. Fremont, who witnessed the event and noted it in his journal. Concerning the calamity he wrote:

A gentleman named Lueders, a botanist from the city of Hamburg, arrived at the bay I have called by his name, while we were bringing up the boats. I was delighted to meet at such a place a man of kindred pursuits; but we had only the pleasure of a brief conversation, as his canoe, under the guidance of two Indians, was about to run the rapids; and I could not enjoy the satisfaction of regaling him with breakfast, which after his recent journey, would have been an extraordinary luxury.

All his few instruments and baggage were in the canoe, and he hurried around to meet it at Grave Yard Bay; but he was scarcely out of sight when, by the carelessness of the Indians, the boat was drawn into the midst of the rapids, and glanced down the river, bottom up, with a loss of everything it contained. In the natural concern I felt for his misfortune, I gave to the little cove the name of Lueders' Bay.

Fremont's note aroused but little interest until Leslie L. Haskins came to Brownsville, Oregon, as a photographer and botanist. As a small boy in

<sup>1</sup> This book is today a part of the library collection of the Oregon Historical Society. Augusta Lueders, a daughter of the German botanist, sent it to Leslie L. Haskins, author of "Wild Flowers of the Pacific Coast," who presented it to the Historical Society library.